



# The white-tailed deer: a keystone herbivore

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## Issues surrounding deer management

During the last 3 centuries, sweeping manipulations of habitat for agriculture, silviculture, and, to a lesser degree, game management have improved and expanded habitat for white-tailed deer (*Odocoileus virginianus*) across much of the landscape in the eastern United States. For most of this century, wildlife managers sought to protect and enhance populations of deer. With the specter of extirpation still haunting their memory, wildlife managers worked hard in the early 20th century to devise and enforce bag limits, short hunting seasons, and buck-only hunts in order to protect the recovering herds. As they professionalized, wildlife managers were quick to follow Leopold's (1933) suggestion that the way to manage game is to manage habitat. For white-tailed deer, this meant favoring edge and early successional habitats by creating gaps and grassy openings in regions dominated by mature forest. Clear-cuts, in particular, continue to be promoted for their immediate production of slash for browse and their ready succession to shade-intolerant species such as aspen (*Populus* spp.) that provide good summer browse, at least for a few years (e.g., Masters et al. 1993, Johnson et al. 1995).

Nearly a decade ago, we warned wildlife professionals and conservation biologists about the ecological consequences of overabundant deer populations (Alverson et al. 1988). Since then, deer populations and their ecological and economic impacts appear to have increased and worsened. As we approach the next millennium, it behooves wildlife managers to contemplate what consequences will result from their actions in their own professional lifetimes. We

hear more each year about the high costs of crop and tree-seedling damage, deer-vehicle collisions, and nuisance deer in suburban locales (Conover et al. 1995). Beyond these substantial economic costs, however, we face new and often vexing issues regarding the ecological costs of overabundant deer. In some cases, it appears that these consequences will extend over decades and perhaps even centuries. This makes it even more important now than it was a decade ago that wildlife managers assume responsibility and take action to minimize the ecological effects of chronically overabundant deer populations.

The wildlife management profession has begun to respond to the economic and ecological impacts of overabundant deer. In 1995, Wisconsin's Bureau of Wildlife elected to scrutinize the impacts of its own deer management policies via a comprehensive Environmental Assessment (VanderZouwen and Warnke 1995). This was the first attempt, that we are aware of, to seriously consider the broad range of ecological and environmental impacts pertaining to a state's deer management policy. Partly in response to this assessment, the Wildlife Bureau also began to institute new hunting regulations in some areas to ensure that more, especially more female, deer were killed (e.g., their 1996 "Earn a Buck" program). This, however, has proved to be a major challenge, both because it is difficult to adjust hunter effort as more areas become off-limits to hunting and because hunters favor a tradition and management they see as contributing to, rather than diminishing, their prospects for personal hunting success. Many hunters remain skeptical about the seriousness of deer impacts, or at least the need to reduce deer densities in their own areas (Diefenbach et al. 1997). Thus, in addition to facing the irony of having done their job too well,

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**Key words:** deer browse, plant diversity, *Odocoileus virginianus*

wildlife managers must now muster the effort to document, and publicize, the negative consequences of overabundant deer if they are to effectively influence hunter effort, which is their primary tool for adjusting deer density.

While managers understand that they can boost deer and other game populations by manipulating habitat, they have been slower to acknowledge the converse, i.e., that managing for abundant deer brings reciprocal effects for their habitats. If our current deer densities adversely affected only a few particularly sensitive species, or if these effects only occurred intermittently (during peaks in deer abundance), or locally (say, in deer yards), then the ecological issues they posed could be addressed via focused and proximate efforts, or perhaps even dismissed as not being a major management issue. Allocating large efforts to document and ameliorate such scattered impacts would appear misguided and wasteful, and traditional approaches to herd management would appear well justified. If instead, however, current deer densities substantially affect many species, and if their impacts are geographically widespread and chronic, then wildlife managers face a different and more serious set of issues (Garrott et al. 1993). In particular, they face the immediate need to accurately monitor and assess the range and nature of these impacts, and, simultaneously, to reset management goals (and perhaps redesign management techniques) to substantially reduce the severity and scale of these impacts.

Here, we review evidence for the contention that chronically high densities of white-tailed deer are having multiple, and often substantial, deleterious ecological impacts across many regions. To structure this review, we specifically consider whether deer are acting as a "keystone" herbivore to substantially alter ecological communities (Paine 1969). We define a keystone species as one that: (1) affects the distribution or abundance of many other species, (2) can affect community structure by strongly modifying patterns of relative abundance among competing species, or (3) affects community structure by affecting the abundance of species at multiple trophic levels. Power et al. (1996) added that keystone species were expected to have disproportionately large impacts on communities. The concept of a keystone species was originally applied to carnivores that affected the relative abundance and competitive interactions among their prey; now, however, most ecologists accept the idea as pertaining to species on any trophic level (Hunter 1992, Paine 1995). With this in mind, we briefly review past and current efforts to assess the nature and severity of the ecological im-

pacts of deer. Considering our 3 criteria for a keystone species, we discuss the impacts of deer on tree seedlings (criteria 1 and 2 above), herbaceous plants (criteria 1 and 2), and species on higher trophic levels (criterion 3). Because we and others have already reviewed much of the older literature elsewhere (Alverson et al. 1988, Warren 1991), we concentrate here on more recent results. While these data remain far from comprehensive, we conclude that ample evidence exists to publicly acknowledge the substantial risks posed by sustaining high deer densities. We therefore conclude by discussing the larger management issues these results raise.

## Effects on trees and shrubs

Wildlife biologists and foresters have known for many years that deer can strongly affect the absolute and relative abundance of woody species (e.g., Leopold et al. 1947, Webb et al. 1956). Such research in trees is both straightforward (involving the tabulation of size or age classes) and of practical importance, given the economic value of trees. Indeed, these effects are so widespread that forestry textbooks have routinely mentioned deer browse as a problem in regenerating particular species (e.g., oaks [*Quercus* spp.]) for years (e.g., Allen and Sharpe 1960).

Some of the best information on tree impacts comes from the Allegheny National Forest in northwestern Pennsylvania, where foresters have long been concerned that high deer densities depress the regeneration of several valuable hardwood species to well below acceptable stocking levels (Harlow and Downing 1970, Marquis 1974, Marquis 1981, Tilghman 1989). Marquis (1975) noted that this region has been heavily browsed since recovery of the deer herds in the 1930s. Suppression or elimination of palatable seedlings and saplings results in a slow but steady conversion of the stand to less-palatable species such as American beech (*Fagus grandifolia*), which is thus given a competitive advantage. Whitney (1984:403) concluded that deer are "one of the more important determinants of forest structure in the Allegheny Plateau over the past 50 years." At very high deer densities and under certain conditions, the seedlings and saplings of all tree species are eliminated and stands with park-like, grass and fern-dominated understories emerge (Fig. 1). Such conditions appear doubly troubling for tree seedlings in that the ferns themselves interfere with the germination, growth, and survival of desirable tree seedlings (Horsley and Marquis 1983), and so may extend the indirect effects of deer browsing on tree regeneration.



Fig. 1. Sustained deer browsing may lead to depauperate understory conditions, as in this scene in a Pennsylvania forest. Such areas are sometimes termed "fern-parks."

Quantitative studies of the effects of deer on the regeneration of tree species and resulting changes in forest composition are becoming common in other areas as well. Robertson and Robertson (1995:68) studied Pennypack Wilderness, a 324-ha natural area northeast of Philadelphia, and concluded that "the striking lack of regeneration by species destined for position in the canopy presages significant structural and compositional shifts in the forest as existing canopy trees die." In suburban areas like this, adverse effects of deer browsing are compounded by the invasion of woody and herbaceous exotic plants and direct human impacts. In a comprehensive assessment of the impacts of deer browsing on forests in central Illinois, Strole and Anderson (1992:141) noted that "deer took a disproportionately large amount of browse from relatively uncommon species" such as white oak (*Quercus alba*) and shagbark hickory (*Carya ovata*). Similarly, in a 10-year study of upland beech-maple (*Fagus-Acer*), lowland ash-elm (*Fraxinus-Ulmus*), and young pin oak (*Q. palustris*) forests in Ohio, Boerner and Brinkman (1996:309) concluded that "deer browsing was more important than environmental gradients or climate factors in determining seedling longevity and mortality." In studying eastern white pine (*Pinus strobus*) at the southern limit of its range in southwestern Wisconsin, Ziegler (1995) noted that although pines have been present for >12,000 years with self-replacement occurring through 1948 (McIntosh 1950), regeneration failures attributable to browsing are now occurring in several stands.

Slow-growing conifers like eastern hemlock (*Tsuga canadensis*) appear particularly sensitive to the sustained effects of deer browsing. Hough (1965) examined changes over a 20-year interval in a

1,620-ha virgin hemlock-hardwood stand in the Allegheny Mountains and noted that deer arrest typical patterns of succession by eliminating the advance regeneration of hemlock seedlings. Similarly, in the upper Midwest, Anderson and Loucks (1979) examined demographic profiles of hemlock and sugar maple in mixed stands and concluded that differential browsing by deer was favoring sugar maples over hemlocks in the smaller size classes. In a follow-up study, Anderson and Katz (1993:203) inferred from enclosure data that enclosure "periods as long as 70 years may be required for shade-tolerant trees to achieve a size class distribution characteristic of all-aged forests." Working in the Porcupine Mountains in Upper Michigan, Frelich and Lorimer (1985) also documented dramatic differences in hemlock regeneration between sites with higher and lower deer densities and predicted that hemlock would be essentially eliminated from stands if browsing levels did not change.

Our own recent research on stands of eastern hemlock and northern white cedar (*Thuja occidentalis*) in northern Wisconsin and western Upper Michigan has confirmed the significant role that deer play in affecting patterns of seedling recruitment (Waller et al. 1996; Fig. 2). We are testing various hypotheses (see Mladenoff and Stearns 1993) that might explain regional patterns of failed regeneration of these 2 eco-

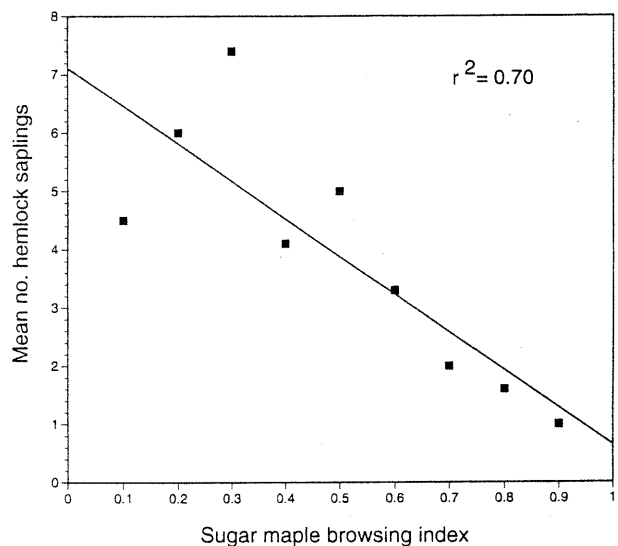


Fig. 2. Declines in the abundance of eastern hemlock (*Tsuga canadensis*) seedlings with increases in local deer browsing. These data reflect the mean abundance of 30–99 cm hemlock seedlings within 14 x 21-m study plots averaged over all study sites within a given browse index class. The browse index at each site was computed from the average proportion of sugar maple (*Acer saccharum*) twigs between 20 and 180 cm high observed to be browsed by deer. Data from 1996 field season (Rooney and Waller unpubl. data).

logically important trees. The presence of small hemlock seedlings at most of our study sites suggests that poor seed production or unsatisfactory sites for initial germination are not limiting seedling recruitment. Other factors traditionally thought to influence seedling abundance, such as stand composition, light, and substrate, also affect the probability of initial seedling establishment. However, numbers of seedlings in larger size classes are for the most part independent of local abiotic conditions and stand composition, but vary strongly across land ownerships in parallel with local deer abundance, as estimated by pellet counts or the browse observed on sugar maple saplings. Results from our experimental exclosures confirm that regional differences in deer abundance account for most of the differential in growth between hemlock seedlings in and outside of these exclosures (Alverson and Waller 1997).

Like hemlock, northern white cedar is a slow-growing, late-successional conifer that often fails to regenerate in northern forests. In response to these failures, the U.S. Forest Service declared a regional moratorium on cutting this important timber species. Conspicuous browse lines, evident in many stands, suggest that deer are an important factor in these failures. Like hemlocks, small cedar seedlings occur disproportionately on "nurse" logs or stumps but suffer high mortality and show few associations with this substrate when older (Scott and Murphy 1987). In a detailed study of a swamp forest, Blewett (1976) concluded that deer were the major limiting factor. We also observe that the size distributions of cedar seedlings differ greatly among nearby ownerships that differ conspicuously in deer density.

Canada yew (*Taxus canadensis*), mountain maple (*Acer spicatum*), yellow birch (*Betula alleghaniensis*), and mountain ash (*Sorbus* spp.) all decreased in apparent response to increasing deer densities in northern Wisconsin (Balgooyen and Waller 1995), as expected given deer browse preferences (Dahlberg and Guettinger 1954, Stiteler and Shaw 1966, Williamson and Hirth 1985). The effects of deer on shrubs such as hobblebush (*Viburnum alnifolium*) are also well documented (Hough 1965, Whitney 1984). Canada yew, an understory shrub of northeastern forests, has long been known to be favored by deer as browse (Beals et al. 1960, Foster 1993). Allison (1990a,b) documented that deer browsing directly affected vegetative cover by yew. He determined also that deer indirectly affected yew's abundance by eating male cones, thereby causing pollen limitation and reducing seed production and reproductive success. *Torreya taxifolia*, a closely related, rare shrub endemic to northern Florida, already ex-

periencing rapid population decline due to fungal infections (Schwartz et al. 1995), is suffering additional losses to antler rubbing by locally abundant deer populations (M. Schwartz, Illinois Nat. Hist. Surv., Urbana, pers. commun.).

## Effects on herbaceous plants

Most of the plant diversity within our forests exists not as trees but rather as herbaceous understory species. Most of these herbaceous plants never grow above the "molar zone" of browse susceptibility and thus are subject to the threat of repeated grazing. In addition, herbaceous plants constitute the bulk of deer summer diets (87%; McCaffery et al. 1974). Finally, whereas the early abundance of tree seedlings and saplings is often discernible through the legacies they subsequently write in the canopy, deer grazing may obliterate herbaceous species without a trace, thereby making it difficult to infer the importance of this factor. Thus, we need careful studies to determine how and where deer may be changing the relative abundances of our native herbs. Although there are few studies on the impacts of deer on herbaceous species, the recent work reviewed here suggests that deer may have substantial and pervasive effects on many herbaceous communities.

Miller et al. (1992) recently compiled reports from both the literature and phone interviews of deer herbivory on 98 rare species. Surprisingly high proportions of rare lilies (40%), orchids (39%), and dicots (56%) were reported to be adversely affected by deer. (They received no reports of adverse effects on rare graminoids.) Many of these accounts were disturbingly dramatic, including the loss of all flowering stems of Loesel's twayblade (*Liparis loeselii*) to grazing in 1984 at an important site for this species in Kentucky, and all flowering stems of the only known population of white fringeless orchid (*Platanthera integrilabia*) in 1989. There were also many accounts of local extirpations caused by deer browsing. Miller et al. (1992) report that such impacts have grown so severe that many conservatory preserves now routinely fence rare or valuable herbs on their property, copying the practice of foresters and orchardists.

Augustine (1997) also noted strongly selective deer preferences for lilies and other monocots in 4 old-growth remnant forests in southeastern Minnesota. He noted that species of *Trillium* and *Uvularia* (both Liliaceae) were favored even after they became scarce. He concluded that deer population densities (which in his study area ranged from 10 to 50/km<sup>2</sup>) were a crucial issue affecting the conservation and

restoration of forest remnants. In Illinois, Anderson (1994) studied the response of *Trillium grandiflorum* to deer browse and proposed that its height could be used to indicate local browse pressure. Inferring from these data, he recommended a density of <4–6 deer/km<sup>2</sup> to retain viable populations of this and similarly palatable herb species. Such selective herbivory also implies that favored species may be overgrazed even when other species show few signs of grazing.

Detailed historical comparisons can provide insight into the dramatic impacts of deer on herbaceous community structure. For example, Rooney and Dress (In Press) observed that hemlock and hemlock-beech stands in Heart's Content, an old-growth forest in northwestern Pennsylvania, lost 59% and 80% of their ground flora species, respectively, between 1929 and 1995. They attributed these losses to the direct and indirect effects of deer herbivory and recommended reducing fern abundance, erecting an enclosure, and reintroducing extirpated species to protect this valuable virgin forest remnant. Drayton and Primack (1996) and Leach and Givnish (1996) noted similarly catastrophic losses from the local floras of Middlesex Fells, outside Boston, and prairie fragments in southern Wisconsin, but inferred no conclusions regarding the role of deer. It is also conceivable that deer could indirectly threaten the persistence of herbaceous species by removing flowers or flowering individuals and so reduce pollen availability and seed set (as with yew) or by reducing populations of pollinators and thus pollinator service (Kearns and Inouye 1997).

In the absence of historical information, inferences about the impacts of deer on herbs are usually drawn by comparing areas known to differ in deer density. Exclosures provide an experimental method to create appropriate controls, but if they were not established before deer became numerous, then they may be of little use as herbs may have already been extirpated. Perhaps more useful, then, are the 'natural experiments' provided by local or regional variation in ambient deer densities. Rooney (1998), for example, compared the density, size, and reproductive condition of a susceptible lily, Canada mayflower (*Maianthemum canadense*), growing on both high and low boulders in the Allegheny National Forest, reasoning that boulders ≥2 m high would act as refuges from deer browsing. He found significantly higher densities (3 times higher than on low boulders), larger plants, and more frequent flowers on high boulder tops in this species, although a second, control, species not susceptible to browse (*Oxalis montana*) showed no such differences.

Balگوoyen and Waller (1995) exploited regional variation in deer densities in northern Wisconsin and the Apostle Islands of Lake Superior to infer both shorter- and longer-term effects of deer browsing on woody and herbaceous communities. We noted declines in several woody plants, overall herbaceous species diversity, and specific declines in wild sarsaparilla (*Aralia nudicaulis*), Canada mayflower, and bluebead lily (*Clintonia borealis*). Whereas the impacts on woody species appeared to be reversible in this study, adverse effects on overall herbaceous diversity persisted for >30 years, with *Clintonia* apparently being extirpated from Madeline Island. Historical effects also were complex in that reductions in deer density allowed recovery of yew on some islands to the point where this coniferous shrub shaded out some herbs. In aggregate, however, both the current and historical effects of deer were strongly negative. Together, these data implied that densities <4.5 deer/km<sup>2</sup> in this region were most compatible with retaining a full complement of herbaceous species. This study was unusual in that it provided a glimpse of how long deer impacts might persist.

Thus, deer have substantial impacts on both particular herbaceous and woody species and overall plant community structure (Fig. 3). For those areas where they still persist, both trillium and bluebead lily serve as convenient indicators of the intensity of deer herbivory. Further long-term monitoring of these and other species could give us a much clearer view of these effects, particularly if steps were taken to assess variation in the intensity and duration of herbivory. Experimental exclosures and reintroductions coupled with models of the long-term effects of shifts in competitive relationships and community structure would also further our understanding. However, the species-specific nature of these responses implies that we may need a considerable body of research to fully assess the range of responses by herbs (and woody plants) to deer herbivory.

## Effects on other trophic levels

Our last criterion for determining if white-tailed deer might be considered a keystone herbivore was that their impacts extend to other trophic levels. Such cascading trophic interactions have been found to be important in aquatic ecosystems (Carpenter 1988).

In his experimental study of the effects of contrasting deer densities on bird populations in Pennsylvania, deCalesta (1994) found that intermediate-

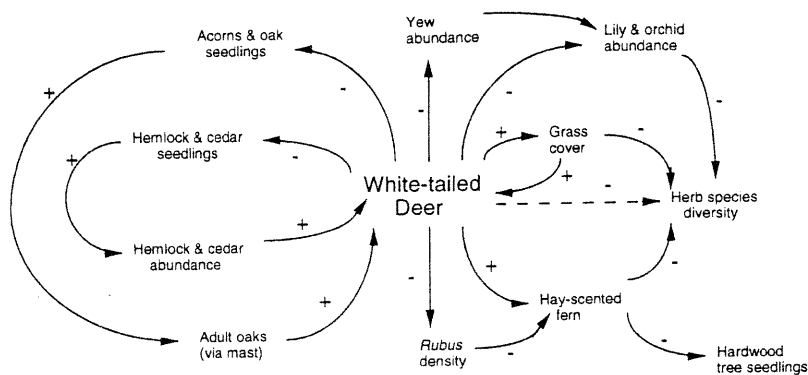


Fig. 3. Documented and inferred interactions of white-tailed deer with various plant species in forests of the northeastern and midwestern United States. Further interactions with species on other trophic levels are not shown (but see Ostfeld et al. 1996). For sources, see text.

These multiple trophic level interactions may extend to include our own species. Elevated deer populations are thought to contribute to the incidence of Lyme disease in humans via the complex interactions of deer ticks (*Ixodes*), white-footed mice (*Peromyscus leucopus*), and spirochaetes (*Borrelia*) that affect the survival and transmission of the disease (Wilson et al. 1985, 1988, 1990; Deblinger et al. 1993; Conover et al. 1995; see also <http://www.lymenet.org>).

## The deer dilemma

canopy-nesting birds declined 37% in abundance and 27% in species diversity at higher deer densities. Five species dropped out at densities of 14.9 deer/km<sup>2</sup> and another 2 disappeared at the highest density of 24.9 deer/km<sup>2</sup>. In contrast, such deer densities did not consistently affect the diversity or abundance of small mammals at these sites (deCalesta, unpubl. rep.).

McShea and Rappole (1992) noted multiple effects at other trophic levels, which prompted them to label deer a keystone species. Casey and Hein (1983) documented losses of 3 bird species in a wildlife-research preserve stocked with high densities of deer, elk (*Cervus canadensis*), and Mouflon sheep (*Ovis aries*). The New Hampshire Natural Heritage Inventory Program similarly reported that deer depressed populations of the Karner Blue Butterfly (*Lycaeides melissa samuelis*), a federally endangered species, by browsing on its lupine host plants (reported in Miller et al. 1992). While expecting deer effects primarily on ground-nesting birds, McShea (1997) found multiple effects on bird species nesting at several levels in the forest, apparently reflecting complex interactions with squirrels (*Sciurus* spp.) and acorn crops. By competing with squirrels and other frugivores for oak mast, deer further affect many other species. For example, squirrel abundance affects rates of bird-nest predation, whereas mice influence the abundance of gypsy moths (Ostfeld et al. 1996). In reviewing these complex interactions in eastern deciduous forests, Ostfeld et al. concluded (1996: 327) that "the complex interactions we have uncovered suggest that it is likely to be difficult or impossible to manage simultaneously for multiple uses (both recreational and industrial) of the forests."

The accumulating body of evidence briefly described here clearly points toward the conclusion that white-tailed deer have reached, and sustained, densities across much of the eastern, northern, and southern United States sufficient to cause manifold and substantial ecological impacts. Furthermore, deleterious impacts on biotic communities have been noted for more than half a century (Leopold 1946). As noted by Power et al. (1996), keystone species are not always of high trophic status, often exert their effects through ecological interactions other than direct consumption, and often only in particular contexts. Impacts of keystone species may also require decades, or centuries, to be fully manifest (Terborgh 1986). By any and all of the criteria we use to define them, white-tailed deer must be accepted as a keystone herbivore in eastern deciduous forests at this time.

Despite numerous studies, over many years and areas, we are only beginning to appreciate in aggregate the biological costs of deer browsing. It is already clear, however, that they are quite large—probably much larger than most wildlife managers expected—and cannot be ignored. Most investigators who have tested for impacts of deer browsing have found them. Many of these impacts have been more dramatic than expected and often more indirect and subtle than expected. Deer browsing clearly favors some species, e.g., hay-scented ferns (*Dennstaedtia punctilobula*) while eliminating others, e.g., Canada yew, often with cascading effects as these intermediary species compete strongly with tree seedlings and herbs. Whereas we have evidence already for these particular interactions (Fig. 3), we can hardly imagine all the ways in which deer browsing will affect patterns of forest diversity once significant shifts in

canopy composition start to occur in response to prolonged failures of regeneration of dominant tree species.

Despite the fact that pernicious deer effects on some plants, birds, and mammals have been manifest for decades, we have been slow in recognizing these effects and appreciating their magnitude. This explains, but only in part, why we have been slow to acknowledge the scale of these impacts and to incorporate this knowledge into more aggressive herd management. With inadequate monitoring, it has been easy to remain (blissfully) unaware of many deer impacts. Yet foresters, orchardists, and other landowners suffering economic losses have been acutely aware of these deer impacts. They often have chosen, however, to address these impacts via proximal solutions, such as browse-proof tubes around individual seedlings and fencing of small areas. Unfortunately, these methods are expensive, limited in extent of application, and do not protect nontarget species.

Taking a larger view, it is evident that our view of deer ecology has centered on *Odocoileus virginianus* itself rather than the web of species it affects. For example, whereas studies of deer forage and range condition are common, studies of collective and cumulative ecological impacts are not. Likewise, we have found it difficult to develop a perspective that transcends local conditions and recent history. We myopically tend to see the elevated deer populations of recent decades as the biological norm, without reference to the conditions under which forest species evolved and adapted over far longer periods of time. Furthermore, the changes deer bring, although chronic and pervasive, are often slow in developing and subtle in appearance. Our ability to detect these subtle changes is impaired by the lack of natural or actual experimental controls for contrast as our landscapes have become increasingly homogenized and subject to high deer populations.

All of this complicates the job of wildlife managers considerably. An originally simple professional mission to accept responsibility and funds to protect the deer herd and provide a steady supply for the hunt has become far more complex. Deer management has forcefully injected wildlife managers into the unexpected and more difficult role of managing habitats and ecosystems. If managers accept responsibility (and income) for managing deer herds, then they must also accept the corresponding duties to understand deer impacts and ameliorate the adverse biological side effects of high deer densities when and where those occur.

## Proposals

We propose 2 courses of action to address the increasing responsibilities of deer managers. The first is to commit firmly to expanding research and monitoring of deer. No manager should be expected to set target deer densities without basic and continuing information on the direct and indirect impacts of management actions. Such monitoring will be especially effective if we can devise efficient and reliable indicators capable of serving as "early warning signs" of impending ecological change. Many of the studies reviewed above are aimed at providing such indicators and could be extended and cross-calibrated. Monitoring efforts should also focus on those elements of the ecosystem likely to be most sensitive to high deer densities, including species such as those whose populations are lowered or eliminated (e.g., orchids) and those whose populations may be inflated (e.g., *Ixodes* and *Borrelia*) so as to affect other species. By necessity, such monitoring should be broad in taxonomic scope because birds, mammals, herpetiles, and invertebrates, as well as herbaceous and woody plants, may be affected. In short, accurate and convenient indicators of ecological impacts should be incorporated into routine management activities.

To accomplish all this, we propose that some reasonable fraction of license revenues (approx 5–10%) specifically be dedicated to devising and implementing comprehensive monitoring programs, including the associated research such programs require. It might also be possible to permit more use of Pittman-Robertson Act funds for this kind of monitoring and research. Although such programs will not be simple to establish, they are clearly needed if we are to have the accurate and timely information we need to pursue adaptive management (Holling 1978, Walters 1986, Nielsen et al. 1997). Fortunately, an increasing cadre of wildlife and conservation biologists appear qualified and eager to participate in these efforts.

Establishing and funding an expanded program for monitoring deer impacts would greatly enhance the information base for managers (as well as providing convincing evidence to hunters and the general public of the extent and severity of such impacts). These efforts must be accompanied, however, by an enhanced ability to use this information to set and adjust deer densities across our contemporary landscapes. Therefore, the second course of action we recommend involves extending our abilities to raise or lower deer populations at various scales. This is, of course, a necessary skill if we are to pursue adaptive management in response to changes in condi-



tions over space and time. It is not yet clear, however, which management practices will best allow managers to manipulate and control deer densities, even locally and temporarily. Although traditional programs for deer management served effectively to protect recovering deer herds and satisfy hunter demand, they have not yet served effectively to correct the excesses of this success. Further experimentation is needed to assess how effectively, and at what scales, deer densities may be reduced by increasing deer kill or by running conventional habitat management "in reverse." We currently lack the technical means to assess population densities at intermediate scales, e.g., townships. We also find that the primary tool for adjusting deer densities (i.e., hunter effort) is heavily constrained by local restrictions on hunting and hunter preferences.

Most state programs assess and manage deer densities over the rather broad geographic scales included in deer management units. Target deer densities are often set at about half the estimated carrying capacity in order to maximize deer population growth rates and, thus, the yield of harvestable animals. Managers often seek to reach such targets throughout each deer management unit and often uniformly among units as well. The homogenous deer densities such management brings, however, may not permit sensitive plant and animal species to escape, even locally or temporarily, from lethal deer-density conditions. At the same time, pervasive changes in contemporary landscapes in favor of edge and disturbed habitats also serve to elevate and homogenize deer densities. Such conditions may well represent a radical departure from historical and prehistorical conditions when deer densities presumably were lower and varied widely in response to landscapes dominated by late-successional species, with more continuous canopy cover, and higher densities of top carnivores.

Sixty years ago, wildlife professionals followed the path blazed by Aldo Leopold, embracing the power of habitat manipulation as a fundamental tool in game management. In the years since then, our awareness of ecological interactions, ecological losses, and our uncertainty have expanded greatly (Alverson et al. 1994). At the same time, our concepts of "wildlife" have broadened to include many more of the organisms sharing a given habitat. The challenge facing wildlife managers today and in the 21st century is to produce and encourage game production in some areas of the landscape without reducing the diversity of wildlife in the broadest sense that share this landscape. These broad conservation goals were enunciated clearly by Leopold in his later years, culminating

in "The Land Ethic" (Leopold 1949:259). We join him in asking: "Can management principles be extended to wildflowers?"

**Acknowledgments.** We thank R. Warren for the invitation to prepare this piece and T. Rooney and R. Warren for their helpful suggestions on an earlier draft of this paper. Support for our field work on hemlock and cedar has come from the NSF (DEB BSR-9000102), the USDA Forest/Rangeland/Crop Ecosystems program (Award #93-00648), and the W.F. Vilas Trust Estate.

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